

# THE EXAMINATION OF THE FEEDING BIOLOGY AND THE HUMIFICATIVE FUNCTION OF DIPLOPODA AND ISOPODA

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## Summary

Author discusses in his paper the results of his research in the feeding biology and the humificative function of the detritophagous diplopodan and isopodan species in the litter of forests. The results of this research can be shortly summed up as follows.

The increase of the weight of the animals in experimental conditions (litter leaves of 16—22 °C, containing 50% of water) is very slow, and never reaches the daily 0,25%.

The animals consumed an amount of litter leaves that corresponded to the 0,5—4% of their live weight (litter leaves in abs. dry weight). This amount is smaller than those given in the literature.

In identical conditions smaller animals consumed relatively more food than the larger ones. On the basis of the Law of Surface, the quotient resulting from the weight of the food consumed daily by the animals, and from the cube root of the square of the weight of the animals, that is, the VAN DER DRIFT constant, is an approximately constant figure, independent of the size of the animals.

The value of the VAN DER DRIFT constant is, in identical conditions, independent not only of the size of the animals but also of its species. Accordingly, it can be deduced that the type of metabolism of detritophagous species of the same habit is essentially agreeing. This circumstance offers some possibility — in the cognizance of the feeding biology of a detritophagous arthropodan species of a given forest — to make deductions concerning the litter-decomposing function of other species of similar habits.

Concurrently with the rise in temperature, the amount of food consumed will also grow rapidly. The optimum lies probably some few grades above 20 °C.

With regard to their metabolism, the species examined show a seasonal cycle, insofar, as their metabolism is more intensive in the spring as in the autumn.

The amount of food consumption is also dependent on the state of decomposition of the litter leaves.

A relatively small proportion of the food consumed (0—7%) is being built into the organism of the animal.

The rate of the utilization of the food material is largely dependent on its state. When the animals were fed with oaken litter leaves taken from layer F<sub>1</sub>, the weight of the excrement reached 87,63—96,23% of the weight of the food consumed, whilst the amount of the material burnt oscillated between 0—9,14%. On the other hand, when they were fed with litter leaves of layer F<sub>x</sub>, the amount of excrement varied only between 79,72—85,04%, and the waste of material reached 9,44—20,54%. Consequently litter leaves from layer F<sub>1</sub> are digested in a lesser rate than those taken from layer F<sub>x</sub>. From the point of view of humification this means that, whereas the litter of layer F<sub>1</sub> when passing through the digestive tracts is being broken up — so to say — mechanically only, the leaves originating from layer F<sub>x</sub> undergo considerable chemical decomposition during the same period.

## Introduction

The literature is uniform in attributing a great importance to the litter-decomposing function of the detritophagous Arthropoda living in the litter stratum of the forest [6, 7, 11, 13, 15, 16]. The relevant views of some authors

are, however, rather different. This should be ascribed primarily to our lack of information concerning the life and metabolism of the animals. The elucidation of this important problem in the productive biology of the forest requires a number of further experiments to be executed according to many new points of view. Their execution and correct evaluation is, however, rendered rather difficult; indeed, well-nigh impossible by a number of special circumstances. In fact the majority of the animals cannot, or can hardly be kept in laboratory conditions, and great many factors must be kept in mind in the course of the evaluation of the results. The metabolism of these animals is influenced by the quality and humidity content of the food, by temperature, season, and by their age not to mention a presumably considerable number of yet unknown factors. Even if all these are kept in mind, the task of correctly applying the data, obtained by measurements, to the natural habitat of the animals still remains unsolved.

The aim of my work was to examine in different laboratory conditions the total food circulation of the most important detritophagous arthropodan species of the macrofauna in the forest floor, thereby to contribute to our knowledge of the life and metabolism of these animals, and to evaluate these data with an eye on the above mentioned difficulties — for further clarification of the humificative function of the animals. Another circumstance that prompted me to undertake this task was — as already pointed out above — the many contradictory instances in the literature.

#### Material and methods

I have selected for my experiments the following three species: *Glomeris hexasticha* BRANDT, *Chromatojulus projectus* VERHOEFF, *Protracheoniscus politus* C. L. KOCH. These diplopodous, that is, isopodous species, as shown by the zoocoenological surveys of BALOGH and LOKSA, generally dominate in our widely ranging Querceto-Potentilletum albae and Querceto-Lithospermetum plant associations, but will frequently occur even elsewhere.

The keeping of the above species in laboratory conditions is not an utterly insolvable task: they may be kept so even for long periods if a suitable litter and soil substratum is secured. Nevertheless the conditions necessarily imposed by experiments, such as the relatively meagre amount of litter and the lack at natural soil substratum, will limit their duration for after a certain time the animals will become ill and show the symptoms of decreasing metabolism. I tried, of course, to make the utmost use of the maximal possibilities: my longest experiment lasted 59 days.

I kept the animals in unglazed earthen pots covered by a sheet of glass, even partly darkened by a bit of cardboard. The bottom of the pots were sunk into the wet sand. According to my experiences, this method is more suitable for the breeding of the animals than the glass dishes, since unglazed earthen vessels will, on the one hand, better guarantee aerial circulation whilst, on the other hand, they will absorb water so that the regulation of the humidity content of the food material can be accomplished by the suitable wetting of the sand, which will, again, prevent the detrimental accumulation of condense water. No sand was put on the bottom of the pots, as it would have hindered the collecting of the excrement, and also because it has proved to have no observable advantageous effect on the life functions of the animals.

I have recorded the weight of the animals both before and after the experiments; the amount of the food material consumed, and the weight of the excrement produced. In order to assure an empty digestive tract, feeding was suspended for 48 hours in both cases and the animals were weighed after fasting. The concurrent establishment of the water content of animals of a size corresponding to the size of those used in the experiments enabled us to convert the weight of the test animals into absolute dry weight.

The animals were fed with oaken litter leaves from a Querceto-Potentilletum albae association. The leaves were selected so as to represent two different phases of decomposition. In some of the experiments, I applied opaque leaves taken from layer F<sub>1</sub>, whilst in some others, faded and translucent ones taken from layer F<sub>x</sub>. Whereas the former had a high content of plasmatic remains, the latter consisted of leaves in the state of a more advanced decomposition, in their bulk consisting of the remnants of cell walls. In every case, I endeavoured to use homogeneous leaf particles which I weighed after a drying process of 2 hours on 104 °C, that is, in an absolute dry state. The weighing of the litter that remained after the experiments was carried out in the same way.

During experiments I kept, in another pot under the same conditions, litter leaves similar to those used for breeding but without any animals feeding on them, to be able to register the changes in their weight brought about by bacteria and fungi. The weight of the litter leaves kept without animals feeding on them showed a considerable decreased. Accordingly, I deduced this loss of weight from the measured amount of litter consumed by the animals and gave this correctional value in the table.

In all experiments I kept the sand, into which the pots were sunk, wet, to ensure a 50% of water content in the food.

The accumulated excrement was removed from the pots once daily, and stored dry, to prevent its secondary decomposition. The amount of excrement that accumulated during the 48 hours of fasting following the experiments was added to the excrement earlier removed.

The test animals were kept on uneven temperature showing daily fluctuations as in the more natural field conditions. The temperature values show the daily average during the experiments; allowing a maximum deviation at  $\pm 1-1,5$  °C according to the different parts of the day.

In my experiments I tried to find answers to the following questions:

1. What is the rate of the increase in weight of the growing animals?
2. What is the amount of food consumed by the animals in certain definite conditions?
3. Does the Law of Surface apply to the quantitative relations of food consumption of small and large individuals, and is there any similarity in the food material consumption of the examined detritophagous species?
4. What is the influence of the quality of food and of the temperature on the feeding of the animals?
5. Is there any seasonal cycle in the metabolism of the animals examined?
6. What is the percentage of the food material the animals build into their organisms, what is the percentage discharged in the form of excrement, and what is the rate of oxydation?
7. What is in the light of the answers to the above questions, the function of the animals in the humification of forest litter?

### Results

The results of all my measurements are summed up in Table 1. Though the number of animals was different in each experiment I have for the sake of easier comparison, calculated the data of weights for one animal in every case. In Experiment 6, I measured the consumption of food and the changes in the weight of the animals in two instances. These data are recorded under 6/1 and 6/2. The excrement accumulated during experiments was measured once only, after the conclusion of the test. The two parts of the experiments were conducted on different temperatures. The absolute dry weights of the animals given for the beginning of the experiments are, naturally, computed

Table 1

Number	Species	Litter layer used for feeding	Time of experiments (season)	Duration of experiments in days	Temperature mean °C	Number of test animals	Live weight of 1 animal at the beginning (mg)		Abs. dry weight of 1 animal at the beginning (mg)		Daily increase in weight of 1 animal		Number of moulted animals	Total weight of moulted chitinous exuviae (mg)	Daily consumption of litter by 1 animal (in abs. dry weight) (mg)	Daily excrement of 1 animal (in abs. dry weight) (mg)
							end (mg)		end (mg)		in live weight (mg)	in abs. dry weight (mg)				
							of the experiment									
1.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	20	21,1	10	53,72	53,91	15,93	15,98	0,0097	0,003	3	8,3	1,67	1,57
2.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	20	21,1	10	50,28	50,90	14,90	15,09	0,031	0,009	2	5,3	1,37	1,29
3.	juv. <i>Glomeris</i> .....	F <sub>x</sub>	autumn	59	17,5	10	53,91	55,46	15,98	16,44	0,026	0,008	4	14,9	0,45	0,37
4.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	14	20,8	10	215,13	216,67	63,78	64,24	0,110	0,033	1	25,3	4,10	3,94
5.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	14	20,8	10	209,76	211,45	62,19	62,69	0,121	0,036	—	—	3,72	3,58
6.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	45	19,5	5	213,07	205,48	63,17	60,92	-0,170	-0,050	3	45,3	2,94	2,75
6/1.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	30	21,0	5	213,07	202,22	63,17	59,95	-0,360	-0,107	3	45,3	3,32	—
6/2.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	15	16,7	5	202,22	205,48	59,95	60,92	0,216	0,060	—	—	2,19	—
7.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	30	21,0	5	198,64	200,13	58,89	59,33	0,049	0,015	1	17,0	4,07	3,87
8.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	spring	11	16,1	3	161,39	165,51	47,85	49,07	0,374	0,111	—	—	2,22	2,12
9.	juv. <i>Chromatojulus</i>	F <sub>1</sub>	autumn	11	21,8	7	125,08	128,02	50,97	52,17	0,267	0,109	—	—	3,38	2,96
10.	juv. <i>Chromatojulus</i>	F <sub>x</sub>	autumn	43	17,4	10	110,34	116,98	44,96	47,67	0,155	0,063	—	—	1,02	0,82
11.	ad. <i>Chromatojulus</i>	F <sub>1</sub>	autumn	41	18,4	5	244,10	227,95	101,86	95,09	-0,390	-0,160	—	—	2,37	2,25
12.	ad. <i>Chromatojulus</i>	F <sub>x</sub>	autumn	43	17,4	1	338,37	349,42	141,20	145,81	0,257	0,107	—	—	1,45	1,15
13.	ad. <i>Chromatojulus</i>	F <sub>x</sub>	autumn	43	17,4	1	178,84	181,69	74,63	75,82	0,066	0,028	—	—	1,34	1,12
14.	ad. <i>Chromatojulus</i>	F <sub>1</sub>	spring	11	15,5	4	231,96	234,89	96,26	97,48	0,266	0,110	—	—	2,08	1,97
15.	ad. <i>Chromatojulus</i>	F <sub>x</sub>	spring	19	15,9	4	178,55	180,88	74,09	75,06	0,123	0,051	—	—	1,01	0,86
16.	juv. <i>Protracheoniscus</i>	F <sub>x</sub>	autumn	21	18,0	10	15,23	15,50	5,01	5,10	0,013	0,004	—	—	0,32	0,26
17.	juv. <i>Protracheoniscus</i>	F <sub>x</sub>	autumn	21	18,0	10	13,95	14,27	4,59	4,69	0,015	0,005	—	—	0,33	0,25
18.	ad. <i>Protracheoniscus</i>	F <sub>x</sub>	autumn	11	18,8	10	38,14	37,95	12,55	12,49	-0,017	-0,006	—	—	0,74	0,63
19.	ad. <i>Protracheoniscus</i>	F <sub>x</sub>	autumn	16	18,5	5	19,89	19,73	6,55	6,49	-0,010	-0,003	—	—	0,39	0,31
20.	ad. <i>Protracheoniscus</i>	F <sub>1</sub>	autumn	15	21,0	10	25,43	25,56	8,37	8,41	0,009	0,003	—	—	1,02	0,97

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values, determined by the average water content of the animals. The average water content of the species is shown in Table 2.

I call special attention to the interesting fact that in a number of cases the weight of the animals after 48 hours fasting increased, instead of decreasing though their intestines had been emptied. So e. g. one adult *Chromatojulus* added 1,1 mg to its weight, five individuals of adult *Protracheoniscus* showed an increase of 0,6 mg in their collective weight and ten specimens of subadult *Protracheoniscus* grew heavier by 1,3 mg in all. The only explanation of this phenomenon I so far can offer is the assumption that the animals took a larger quantity of water at such times.

I summed up the data concerning the daily changes in the weight of the animals in Table 3. They are given in percentages computed from the values of the animal's weight measured at the beginning of each experiment irrespectively of its duration. This may involve some errors, because in calculating the percentages I disregarded the daily changes in the weight of the animals. Nevertheless this method prove sufficiently exact since the weight of the animals changed but little during the period of the experiments as seen in the Table. Within the limits of the daily fluctuations of temperature (16—22 °C) the growth of the animals was so slow that their daily gain in weight never reached 0,25 %. Greater differences between the rates of the growth of the three species can not be shown, but the slight differences to be found can be explained by the different susceptibility of the respective species to laboratory conditions. The data thus obtained enable us to draw conclusions only with the greatest reservation concerning the growth of the animals in natural conditions, though one thing is certain: their growth is considerably slow also in field conditions. If we suppose that the *Glomeris* specimens, which were the easiest to raise, increased their weight daily by 0,1% then 838 days were needed for their complete development. My basis here was 0,9 mg live weight at the time of hatching and 200 mg at the time of full development. This length of time seems to be a pretty correct estimate, as for instance KÜKENTHAL puts the life span of Diplopoda at 3 years.

In addition the *Glomeris* specimens even moulted during the experiments. According to my observations, each individual moulted every hundred days (computed by statistical data). I will also mention the fact that though the *Protracheoniscus* used in these experiments did not moult, individuals belonging to this species did moult in the course of other tests. In the case of *Chromatojulus* specimens on the other hand moulting occurred but exceptionally. Occasionally I have recorded a certain decrease in the weight of some adult animals. It can be inferred from these observations that after the attainment of a certain size the weight of the animals will not or will but very slightly increase.

Table 4 shows the daily amount of food consumed by the animals bred in the autumn, expressed by percentages of their initial live weight and absolute

Table 2

Species	<i>Glomeris hexasticha</i>	juv. <i>Chromatojulus projectus</i>	ad. <i>Chromatojulus projectus</i>	<i>Protracheoniscus politus</i>
Water content of animal (related to abs. dry weight).....	70,35%	59,25%	58,27%	67,09%

Table 3

Number	1.	2.	3.	4.	5.	6.
Species	juv. <i>Glomeris</i>	juv. <i>Glomeris</i>	juv. <i>Glomeris</i>	ad. <i>Glomeris</i>	ad. <i>Glomeris</i>	ad. <i>Glomeris</i>
Daily change in weight of 1 animal, in percentage of initial live weight .....	0,018	0,062	0,049	0,051	0,057	-0,079
Number of animals moulted during experiments .....	3 of 10	2 of 10	4 of 10	1 of 10	-	3 of 5

Number	6/1.	6/2.	7.	8.	9.	10.
Species	ad. <i>Glomeris</i>	ad. <i>Glomeris</i>	ad. <i>Glomeris</i>	ad. <i>Glomeris</i>	juv. <i>Chromato- julus</i>	juv. <i>Chromato- julus</i>
Daily change in weight of 1 animal, in percentage of initial live weight .....	-0,170	0,106	0,025	0,230	0,210	0,140
Number of animals moulted during experiments .....	3 of 5	-	1 of 5	-	-	-

Number	11.	12.	13.	14.	15.
Species	ad. <i>Chromatojulus</i>	ad. <i>Chromatojulus</i>	ad. <i>Chromatojulus</i>	ad. <i>Chromatojulus</i>	ad. <i>Chromatojulus</i>
Daily change in weight of 1 animal, in percentage of initial live weight .....	-0,160	0,076	0,037	0,110	0,069
Number of animals moulted during experiments .....	-	-	-	-	-

Number	16.	17.	18.	19.	20.
Species	juv. <i>Protracheo- niscus</i>	juv. <i>Protracheo- niscus</i>	ad. <i>Protracheo- niscus</i>	ad. <i>Protracheo- niscus</i>	ad. <i>Protracheo- niscus</i>
Daily change in weight of 1 animal, in percentage of initial live weight .....	0,084	0,110	-0,045	-0,049	0,034
Number of animals moulted during experiments .....	-	-	-	-	-

Table 4

Number	Species	Litter layer used for feeding	Temperature mean °C	Live weight of 1 animal (mg)	Abs. dry weight of 1 animal (mg)	Daily consumption of litter (abs. dry weight) by 1 animal in percentage of its initial		Value of the VAN DER DRIFT constant
						at the beginning of experiments	live weight	
6/2.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	16,7	202,22	59,95	1,08	3,65	0,14
3.	juv. <i>Glomeris</i> .....	F <sub>x</sub>	17,5	53,91	15,98	0,83	2,82	0,071
6.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	19,5	213,07	63,17	1,38	4,65	0,18
4.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	20,8	215,13	63,78	1,91	6,43	0,26
5.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	20,8	209,76	62,19	1,77	5,98	0,24
6/1.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	21,0	213,07	63,17	1,56	5,25	0,21
7.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	21,0	198,64	58,89	2,05	6,91	0,27
1.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	21,1	53,73	15,93	3,11	10,48	0,26
2.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	21,1	50,28	14,90	2,72	9,17	0,23
10.	juv. <i>Chromatojulus</i> .....	F <sub>x</sub>	17,4	110,34	44,96	0,93	2,28	0,081
12.	ad. <i>Chromatojulus</i> .....	F <sub>x</sub>	17,4	338,37	141,20	0,43	1,03	0,054
13.	ad. <i>Chromatojulus</i> .....	F <sub>x</sub>	17,4	178,84	74,63	0,75	1,79	0,076
11.	ad. <i>Chromatojulus</i> .....	F <sub>1</sub>	18,4	244,10	101,86	0,83	2,82	0,11
9.	juv. <i>Chromatojulus</i> .....	F <sub>1</sub>	21,8	125,08	50,97	2,70	6,63	0,24
16.	juv. <i>Protracheoniscus</i> .....	F <sub>x</sub>	18,0	15,23	5,01	2,07	6,31	0,11
17.	juv. <i>Protracheoniscus</i> .....	F <sub>x</sub>	18,0	13,95	4,59	2,38	7,21	0,12
19.	ad. <i>Protracheoniscus</i> .....	F <sub>x</sub>	18,5	19,89	6,54	1,96	5,96	0,11
18.	ad. <i>Protracheoniscus</i> .....	F <sub>x</sub>	18,8	38,14	12,55	1,94	5,91	0,14
20.	ad. <i>Protracheoniscus</i> .....	F <sub>1</sub>	21,0	25,56	8,37	4,01	12,19	0,25

dry weight. It will be seen that the animals consumed a rather small amount of leaves, a daily 0,5—4% of their live weight only. (Litter leaves measured in absolute dry weight.) This value is lower than what the one recorded in the literature [5]. VAN DER DRIFT carried on similar experiments with the species *Glomeris marginata* VILLERS and *Cylindrojulus silvarum* MEINERT [14]. He kept adult specimens of the former species at 18 °C, fed them with leaves of 55% water content, and found that they had consumed a daily 5,2% of their live weight. Bred on leaves of a higher (70%) water content, the animals consumed daily 9—21% of their live weight. He found the amount of food consumed by *Cylindrojulus silvarum* to be only slightly less. (The above numbers are the converted values of VAN DER DRIFT's data who measured food in aerial dry weight and recorded the amount consumed during more than one day.)

It is difficult to interpret correctly the above differences in the amount of food consumed. Though there is a possibility that the metabolism of my animals, owing to long captivity, decreased and so my figures are below the values of those in natural conditions, yet, on the other hand, I should consider it a source of error in VAN DER DRIFT's experiments that they lasted but for a short period (5 days). Because of the previous fasting the animals possibly consumed more food than under normal circumstances, a supposition which seems to be supported by my observations.

It can also be seen from Table 4 that — as stated by VAN DER DRIFT [14] — the smaller (younger) specimens of the identical species consume relatively more food than the larger (adult) ones; the quantity, however, of the food

consumed is in proportion to the active surface of the consumers. The surface of the young ones is relatively larger, that of the adult ones smaller. The active surface of the animals is usually expressed by the formula  $\sqrt[3]{g^2}$ , that is  $g^{2/3}$ , where  $g$  equals the weight of the animals, in this case their initial absolute dry weight. In the last column of Table 4 I give the quotient of the daily amount of food consumed (expressed in absolute dry weight) and of the cube-root extracted from the square of their weight, which we call, with BALOGH [1], the VAN DER DRIFT constant. According to what was said above, this value must be a constant, independent of the size of the animal. This can be ascertained from Table 4, if we compare animals bred on identical food and kept on identical or almost identical temperature. Thus, for instance, the VAN DER DRIFT constant oscillates between 0,21—0,27 in the case of *Glomeris* specimens (Experiments 4, 5, 6/1, 7, 1, 2), between 0,054—0,081 in the case of *Chromatojulus* specimens (Experiments 10, 12, 13), and between 0,11—0,14 with *Protracheoniscus* specimens (Experiments 16, 17, 18, 19). These values move within rather close limits, only the largest individual among the *Chromatojulus* specimens shows a considerably smaller figure. This same phenomenon was observed also by VAN DER DRIFT [14] who, too, attributes it to the decreased metabolism of a senescent organism.

If we compare the VAN DER DRIFT constants of animals belonging to different species, we find that the VAN DER DRIFT constant (0,071) of *Glomeris* specimens kept at 17,5 °C in Experiment 3 can be inserted between the VAN DER DRIFT constant values (0,054—0,081) of *Chromatojulus* specimens bred at a temperature of 17,4 °C, and that this constant (0,24) of the *Chromatojulus* species (bred at 21,8 °C in Experiment 9) and that (0,25) of the *Protracheoniscus* specimens (bred at 21,0 °C in Experiment 20) can be inserted between the 0,21—0,27 VAN DER DRIFT constant values of *Glomeris* specimens (kept at 20,8—21,1 °C). These figures show that the type of metabolism of species belonging to the same habits is by and large analogous. This applies to species systematically so distant as are Diplopoda from Isopoda. Hence I presume that the quotient of the amount of food consumed and of the 2/3 power of the weight, that is, the VAN DER DRIFT constant of animals having the same habit living in similar biocoenoses is, irrespective of the species and of the size of the single individual, in identical climatical (season, temperature, humidity, etc.) conditions and consuming identical food is indeed invariable. Not even the form of the animals will influence the above statement. Some of the experiments seem to show that the VAN DER DRIFT constant of *Chromatojulus* specimens is slightly lower than that of the two other species (in similar conditions) but this can again be explained by the assumption that these animals will endure laboratory conditions less easily.

Among others, BORNEBUSCH [4], BUDDENBROCK [3, p. 202], BERTALANFFY [3], and MÜLLER [3, p. 202] also discussed the VAN DER DRIFT constant. As

to the validity of this constant, their opinions are different. Some of them contest whether it holds good for the individuals of different species, others again doubt its applicability to specimens of different size within the same species.

Table 4 gives also good evidence of the fact that changes in temperature have a strong influence upon the intensity of metabolism. On the basis of what has been said above, the VAN DER DRIFT constant also lends itself to express metabolical changes effected by temperature, under identical conditions including food consumption. I have, therefore, grouped in Table 5 the VAN DER DRIFT constants obtained from the food consumption of animals bred in the autumn so as to form two groups according to the two kinds of food used in the experiments, and within these two groups in the succession dictated by the increasing temperature values.

Table 5

Feeding litter from layer F <sub>1</sub>	Number	6/2.	11.	6.	4.	5.	20.	6/1.	7.	1.	2.	9.
Temperature mean		16,7	18,4	19,5	20,8	20,8	21,0	21,0	21,0	21,1	21,1	21,8
Value of the VANDER DRIFT constant		0,14	0,11	0,18	0,26	0,24	0,25	0,21	0,27	0,26	0,23	0,24

Feeding litter from layer F <sub>x</sub>	Number	10.	12.	13.	3.	16.	17.	19.	18.
Temperature mean		17,4	17,4	17,4	17,5	18,0	18,0	18,5	18,8
Value of the VANDER DRIFT constant		0,081	0,054	0,076	0,071	0,11	0,12	0,11	0,14

The amount of food consumed will show a rapid growth in rising temperature. VAN DER DRIFT, on the basis of his experiments, places the temperature optimum of the species he examined between 17,5—22,5 °C. The temperature optimum of the species used in my experiments will probably be higher, as food consumption showed a strong increase even between 19,5—21,0 °C. This is presumably due to the fact that, though the winter in the Netherlands (where the animals examined by VAN DER DRIFT come from) is somewhat warmer than in Hungary, the temperature of the warm season — most important from the point of view of the active work of the animals — will rise higher in our country (the average temperature of the warmest month in Amsterdam, August, is 18,7 °C, whilst that of our hottest month, July, is 21,9 °C in Budapest).

The relatively low value of the VAN DER DRIFT constant of the animals used in Experiment 11 can be explained by the sickness of the animals, apparent also in the striking loss of their weight.

The Table shows also that the animals that were fed with the litter of layer  $F_1$ , consumed more foodstuff than those fed on the leaves of layer  $F_x$ . The quantity of the food consumed will, therefore, be influenced by its quality, that is by the rate of decomposition of the foodstuff.

Table 6

Number	Species	Layer of litter used for feeding	Temper- ature mean °C	Live weight of 1 ani- mal (mg)	Abs. dry weight of 1 animal (mg)	Daily consumption of litter (abs. dry weight) by one animal in per- centage of its initial		Value of the VAN DER DRIFT constant
				beginning of experiments		live weight	abs. dry weight	
14.	ad. <i>Chromatojulus</i>	$F_1$	15,5	231,96	96,26	0,89	2,16	0,099
15.	ad. <i>Chromatojulus</i>	$F_x$	15,9	178,55	74,09	0,57	1,37	0,057
8.	ad. <i>Glomeris</i>	$F_1$	16,1	161,39	47,85	1,38	4,64	0,17

Experiments 8, 14, 15, the consumption data of which are shown on Table 6, were performed in the spring. This enables us to examine also the effect of the seasons on metabolism. The figures, and mainly the values of the VAN DER DRIFT constant, go to show that the metabolism of the animals is higher in the spring than in the autumn. Experiment 14 (at 15,5 °C) will not be at the value of the VAN DER DRIFT constant, fall much short at the value of the VAN DER DRIFT constant in Experiment 6/2 (at 16,7 °C); the value of the VAN DER DRIFT constant in Experiment 15 (at 15,9 °C) approaches the one measured at 17,4 °C in the autumn, whilst the value of the VAN DER DRIFT constant in Experiment 8 (at 16,1 °C) comes close to the one measured in the autumn (at 19,5 °C). Therefore, a definite seasonal cycle can be observed in the metabolism of the animals. Finally, the effect of the quality of the food material, described in the discussion of the experiments made in the autumn, can be ascertained in these cases.

The data given in Table 7 show the rate of the utilization of the food material taken by the animals. They will tell us how much of 100 absolute dry weight of food was built into the organism of the animals, how much was discharged as excrement, and, finally, what is the amount of the "material wasted" by way of oxydation.

It can be stated that the "building in" of the food into the organism is limited to a maximum of 7%, including even the chitinous exuviae of the moulted animals. Sometimes with adult specimens the food serves exclusively for the maintenance of metabolic processes. The proportion of the produced excrement and the waste as related to the food shows a striking difference according to the quality of nutriment. The percental rate of the excrement of animals fed on litter from layer  $F_1$  is high (87,63—96,23%), with a concur-

Table 7

Number	Species	Layer of litter used for feeding	Time of experiment (season)	Temper-ature mean °C	Amount (in abs. dry weight, and in percentage of abs. dry weight of the food material) of			
					the material built into the body of the animals	the moulted exuviae	the excre-ment	the „waste of material”
1.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	21,1	0,17	2,48	93,81	3,53
2.	juv. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	21,1	0,66	1,94	94,65	2,75
8,	ad. <i>Glomeris</i> .....	F <sub>1</sub>	spring	16,1	4,99	—	95,59	+0,58
6.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	19,5	-1,69	6,83	93,51	1,35
4.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	20,8	0,78	4,41	96,04	+1,23
5.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	20,8	0,97	—	96,23	2,80
7.	ad. <i>Glomeris</i> .....	F <sub>1</sub>	autumn	21,0	0,36	1,39	95,13	3,12
9.	juv. <i>Chromatojulus</i> .....	F <sub>1</sub>	autumn	21,8	3,22	—	87,63	9,14
14.	ad. <i>Chromatojulus</i> .....	F <sub>1</sub>	spring	15,5	5,31	—	94,94	+0,25
11.	ad. <i>Chromatojulus</i> .....	F <sub>1</sub>	autumn	18,4	-6,93	—	94,83	12,10
20.	ad. <i>Protracheoniscus</i> ...	F <sub>1</sub>	autumn	21,0	0,27	—	94,88	4,85
3.	juv. <i>Glomeris</i> .....	F <sub>x</sub>	autumn	17,5	1,69	5,61	83,26	9,44
10.	juv. <i>Chromatojulus</i> .....	F <sub>x</sub>	autumn	17,4	6,14	—	80,09	13,77
15.	ad. <i>Chromatojulus</i> .....	F <sub>x</sub>	spring	15,9	5,01	—	85,04	9,95
12.	ad. <i>Chromatojulus</i> .....	F <sub>x</sub>	autumn	17,4	7,39	—	79,72	12,89
13.	ad. <i>Chromatojulus</i> .....	F <sub>x</sub>	autumn	17,4	2,04	—	83,50	14,46
16.	juv. <i>Protracheoniscus</i> ...	F <sub>x</sub>	autumn	18,0	1,32	—	82,91	15,77
17.	juv. <i>Protracheoniscus</i> ...	F <sub>x</sub>	autumn	18,0	1,44	—	81,31	17,25
19.	ad. <i>Protracheoniscus</i> ...	F <sub>x</sub>	autumn	18,5	-0,80	—	80,26	20,54
18.	ad. <i>Protracheoniscus</i> ...	F <sub>x</sub>	autumn	18,8	-0,76	—	84,89	15,87

rently low rate of waste (0—12,10%), whilst the weight of the excrement related to the food consumed by animals fed on litter from layer F<sub>x</sub> is much less (79,72—85,04%), — and so the waste is even higher (9,44—20,54%). In this connection I have to mention that, if we disregard the result of Experiment 11, the above difference will be even more marked, as the waste within the former groups will decrease to 0—9,14%. The exclusion of Experiment 11 from this discussion is justified by the fact that the waste in this case was the consequence of the strong decrease in the weight of the animals which, in turn, should be ascribed to their probable sickness as mentioned above. The slight material surplus showing up in some cases in the metabolism of animals fed on litter leaves of layer F<sub>1</sub> is probably the result of experimental error.

In my opinion these data will bring to an issue the debate which arose about the function of these animals in the decomposition of the litter. According to the analyses of FRANZ and LEITENBERGER [8], who fed diplopods on freshly fallen leaves, the excrement of the animals exhibited a considerable rate of humification. VAN DER DRIFT [14] on the contrary, found the excrement of animals fed on litter leaves of layer F<sub>1</sub> to be in a state of humification only slightly above that at the food consumed.

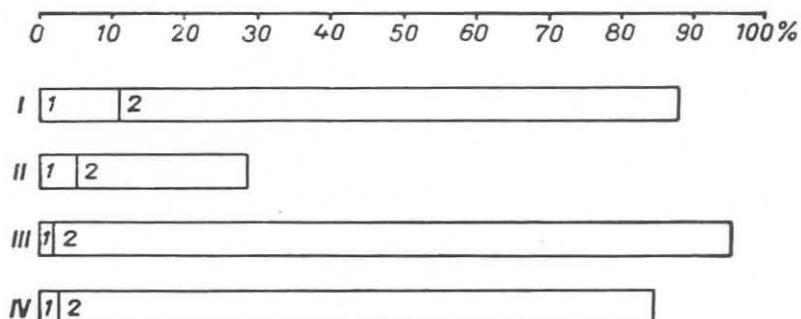
If we take into consideration that the waste of material in the metabolism of the animals is the function of the intensity of decomposition, we may rightly

assert that the rate of the humifying processes taking place in the intestinal canals of the animals varies in accordance with the chemical composition and the state of the food consumed. Accordingly, the differences in the results obtained by FRANZ and LEITENBERGER, on the one hand, and by VAN DER DRIFT on the other, may be ascribed to the different state of the litter leaves fed to the animals. The difference in the decomposition of different food materials still remains to be explained. Though it is easier to imagine that the animal utilizes a more adequate food more intensively, which then involves a greater amount of waste, still I concur with VAN DER DRIFT in the assumption that the higher amount of waste emerges in the case of the consumption of a less adequate food. In the leaves of layer  $F_1$  there may be chemical compounds in a state of decomposition as will render the food material easily utilizable. After the utilization of the food and the discharge of the remnants there is a new possibility for the intake of fresh food. These compounds will not yet have come into existence in the freshly fallen litter, nor can they be found any longer in the litter of layer  $F_x$ , and consequently in both cases, the food has to undergo greater chemical changes in the intestines to become utilizable for the animals. This, again, involves a slower defecation. This assumption, however, — though in want of thorough physiological elucidation — seems to be supported by the observation that the animals consumed less food from the litter of layer  $F_x$  the consumption of which resulted in a higher amount of waste than from the litter of layer  $F_1$  whilst freshly fallen litter undergoing strong decomposition after consumption as shown by FRANZ and LEITENBERGER is indeed reluctantly consumed by the animals.

From the point of view of productive biology the most important point is to know the different courses of the food consumed. Comparing them with the total food circulation of Arthropoda feeding on other kinds of vegetable matter, we find a characteristical excess of the weight rate of the excrement over the proportion of the material built into the organism. In the case of caterpillars of *Hyphantria cunea*, an animal feeding on live plant material (a primary consumer), I found together with BALOGH [2] that the animals had, during their development turned 77,5% of the food into excrement, built 11,5% into their bodies, and used 11,0% to cover the energy necessary for lifefunctions. I found this proportion to be shifted in favour of building in purpose in the case of *Ephestia kuehniella* caterpillars, fed on meal, a dry vegetable material [10]. Here, apart from the extraordinary metabolism previous to pupation, the building in was 5,4%, with a concurrent excremental weight of 23,3%, at a temperature of 26—27 °C. (The high value of waste — 71,3% — is caused by the burning of the meal to ensure the necessary amount of water.) The mean values for the animals discussed in this paper, are as follows: 2,3% of the amount of food is built into the organisms, 94,3% is turned into excrement and 3,4% into waste in the case of feeding on litter leaves from layer  $F_1$ ; this pro-

portion changes to 3,2 : 82,3 : 14,5 when feeding on litter from layer  $F_x$ . (All figures related to the absolute dry weight of the food consumed). Graph 1 will make more conspicuous what has been said above.

These animals turn a strikingly large proportion of the food consumed into excrement, hastening thereby the decomposition of the litter store of the biocoenoses, that is, the coenoses of the litter stratum. The frequently contradictory data in the literature concerning the function of these animals must, however, be reevaluated to a certain extent on the basis of my recent researches. I wish to make clear, on the one hand, that, albeit the function of the detrito-



Graph 1

I. *Hyphantria cunea* Drury, II. *Ephestia kuehniella* Z, III. Diplopoda and Isopoda, feeding on litter leaves from layer  $F_1$ , IV. Diplopoda and Isopoda, feeding on litter leaves from layer  $F_x$ . The abs. dry weight proportions of materials built into the bodies of the animals [1], and the abs. dry weight proportions of excrement [2] related to the abs. dry weight of food consumed

phagous macrofauna of the forest litter consists primarily in the enlargement of the surface by breaking up the food, their part played in the chemical decomposition must in certain conditions still be looked upon as also rather significant; on the other hand, that according to the data relating to the quantitative proportions of food consumption, the amount of litter consumed yearly by the macrofauna in our forests is essentially smaller than has been supposed to be. Nevertheless I do not consider our present knowledge sufficient for the numerical computation of the consumed litter material. Yet it is my profound conviction that our orientation along this line will be facilitated by the specific independence of the VAN DER DRIFT constant, because the use of this constant enables us to infer the amount of food consumed by all detritophagous species from the food consumed by the individuals of any size belonging to a detritophagous arthropodan species living in the same plant association.

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ИССЛЕДОВАНИЕ БИОЛОГИИ ПИТАНИЯ DIPLOPODA И ISOPODA  
И ИХ РОЛИ В ГУМИФИКАЦИИ

Описывается работа по биологии питания и роли в гумификации гниепоедающих видов Diplopoda и Isopoda, живущих в ярусе лесной подстилки. По данным прибавление веса животных в экспериментальных условиях идет чрезвычайно медленно, во всех случаях меньше 0,25% в день. Животные каждый день поедали соответствующий 0,5—4% живого веса своих тел подстилочный лист. Это количество меньше чем, которое указывается в литературе. Животные, обладающие меньшим объемом тела, по сравнению с животными, обладающими более большим размером, в тождественных условиях поедают больше питательных веществ. По закону поверхности констант *Van der Дрифта* (VAN DER DRIFT) (частное от веса поедаемого питательного вещества в день животными и от кубического корня квадрата живого веса) независит от величины животных, а приблизительно является постоянным числом. Величина константы *Van der Дрифта* в тождественных условиях не зависит не только от величины животных, но и от их видовой принадлежности. Это дает возможность нам при знании биологии питания одного гниепоедающего членистоногих сделать заключение по поводу деятельности других видов в расщеплении листьев лесной подстилки.

При повышении температуры быстро повышается потребление в пище. С этой точки зрения оптимум наверно находится на несколько градусов выше 20°C. Исследуемые виды показывают древнейший цикл, поскольку обмен веществ у них весной идет более интенсивно, чем осенью. Количество всасываемой части пищи зависит и от меры распада (гниения) листьев лесной подстилки. Только незначительная часть принимаемой пищи, всего 0,7% становится потом составной частью самого организма. Степень употребления пищи зависит от самих питательных веществ. Питая животных дубовой подстилкой, получаемой из яруса F<sub>1</sub>, вес экскремента (фекалии) достиг 87,63—96,23% всего принимаемого питательного вещества, вес оксицируемого вещества 0—9,14%. Напротив, питая животных листьями лесной подстилки из яруса F<sub>x</sub> экскремент (фекалия) был всего около 79,72—85,04%, а нужда в питательных веществах возросла на 9,44—20,54%. Итак,

листья лесной подстилки из яруса  $F_1$  животные могут переваривать только в меньшей степени, чем листья лесной подстилки из яруса  $F_x$ .

С точки зрения гумификации это значит, что пока опавшая листва из яруса  $F_1$ , переходя через кишечник размельчается только механически, опавшая листва из яруса  $F_x$  за это же время претерпевает значительное химическое изменение.

## UNTERSUCHUNG DER ERNÄHRUNGSBIOLOGIE DER DIPLOPODEN UND ISOPODEN UND IHRE ROLLE IN DER HUMIFIKATION

Es werden die Ergebnisse der Untersuchungen betreffend Ernährungsbiologie und Rolle bei der Humifikation saprophytischer Diplopoda- und Isopodaarten der Karstschicht des Waldbodens mitgeteilt. Die Untersuchungen ergaben, dass die Gewichtszunahme der Tiere unter Laboratoriumsbedingungen sehr gering ist, in allen untersuchten Fällen weniger als 0,25% pro Tag.

Die Tiere frasssen täglich 0,5—4% ihres Leibengewichtes. Diese Quantität ist geringer, als die bisher publizierten Angaben. Unter gleichen Bedingungen frasssen kleinere Tiere relativ mehr, als grössere. Entsprechend des Oberflächengesetzes ist die VAN DER DRIFT'sche Konstante (Gewicht der täglich aufgenommenen Nahrung dividiert durch die Kubikwurzel des Quadrates des Leibengewichtes) eine von der Körpergrösse des Tieres unabhängige, annähernd konstante Zahl.

Der Wert der VAN DER DRIFT'schen Konstante ist unter gleichen Bedingungen nicht nur von der Grösse, sondern auch von der Artzugehörigkeit des Tieres unabhängig. Dieser Umstand erlaubt aus der Ernährungsbiologie einer saprophytischen Arthropodenart irgendeines Waldes Schlussfolgerungen zu ziehen über die Abbautätigkeit anderer Arten der gleichen Lebensweise.

Mit steigender Temperatur nimmt die Nahrungsaufnahme der Tiere schnell zu. Das Optimum dürfte etwas über 20° C liegen.

Die untersuchten Arten zeigten einen Saisonzyklus des Stoffwechsels. Der Stoffwechsel war im Frühjahr lebhafter, als im Herbst.

Die Grösse der Nahrungsaufnahme ist auch vom Verwesungsgrad der Blätter abhängig. Nur ein relativ sehr geringer Anteil, 0—7% der aufgenommenen Nahrung wird in den tierischen Körper eingebaut.

Das Mass der Ausnutzung der Nahrung ist weitgehend von ihrer Qualität abhängig. Wurden die Tiere mit Eichenlaub aus der  $F_1$  Schicht gefüttert, so betrug das Gewicht des Faeces 87,63—96,23% der aufgenommenen Nahrung, das Gewicht der verbrannten Stoffe dementsprechend 0—9,14%. Wurden dagegen die Tiere mit Blättern aus der  $F_x$  Schicht ernährt, schwankt der Faeces zwischen 79,72—85,04% und der Nährstoffmangel stieg auf 9,44—20,54%. Die Tiere verdauen also Blätter aus der ersten Schicht in viel geringerem Masse, als Blätter aus der letztge nannten Schicht. Für die Humifikation bedeutet dies, dass die Blätter der  $F_1$  Schicht auf dem Wege durch den Verdauungstraktus des Tieres nur mechanisch zerkleinert werden, während Blätter aus der  $F_x$  Schicht auf demselben Wege einen weitgehenden chemischen Abbau erfahren.

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